



The Legacy and Continuity of Forest Disturbance, Succession, and Species at the MOFEP Sites

Richard Guyette¹ and John M. Kabrick²

Abstract.—Information about the scale, frequency, and legacy of disturbance regimes and their relation to the distribution of forest species is sparse in Ozark ecosystems. Knowledge of these relationships is valuable for understanding present-day forest ecosystem species composition and structure and for predicting how Missouri's forests will respond to management. Here, we generate a correlation matrix of diverse variables to evaluate the hypothesis that plant and animal species abundances at MOFEP are closely linked to historic disturbance regimes induced by long-term interactions between humans and topographic roughness. Abrupt ring-width reductions in shortleaf pine, fire frequency, and historical data were used to determine the frequency of disturbance. Disturbance variables are correlated with topographic roughness, forest bird territory density, lizard and skink captures, blueberry fruit abundance, *Armillaria* spp. abundance, and three indices of forest succession derived from overstory tree species, oak overstory species, and tree species ground flora. Disturbance history, species distributions, and tree species diversity at the MOFEP sites support the argument that long-term disturbance regimes and successional sequences are major factors affecting species and structure in Ozarks forests.

The Missouri Ozark Forest Ecosystem Project (MOFEP) is a long-term study initiated to quantify the effects of standard forest management practices on forest flora and fauna (Brookshire *et al.* 1997, Brookshire and Hauser 1993, Kurzejeski *et al.* 1993). As such, MOFEP is focused on how the contemporary Ozark forest responds to silvicultural disturbances. Considerable effort has been devoted to quantifying contemporary plant and animal species distributions and ecosystem processes (cf. Brookshire and Shifley 1997). However, our understanding of the contemporary Ozark forests may be incomplete without knowledge of the natural and anthropogenic disturbances

that created these forests. For example, extensive timber harvests during the late 1800s and early 1900s followed by wildfire and overgrazing removed most of the native shortleaf pine (*Pinus echinata*) in the Ozarks (Cunningham and Hauser 1989, Galloway 1961, Krusekopf *et al.* 1921). Guyette and Dey (1997) estimated that the contemporary forests at MOFEP site 8 contain 66 percent less shortleaf pine than the pre-European forests. Moreover, there is evidence that natural and anthropogenic fire was an important disturbance of the pre-European forests in the MOFEP study sites (Guyette and Cutter 1997). These fires certainly affected forest composition, structure, and ecosystem function long before Europeans settled this region.

In addition to ecological significance, the scale, frequency, and legacy of disturbance regimes and their effects on the distribution of forest species also have important management, policy, and political implications. Debates about clearcutting versus selective cutting often hinge on what is "natural," or what was the pre-European disturbance regime. Managers and policy makers are often interested in mimicking

¹ Research Associate Professor, The School of Natural Resources, 203 ABNR, University of Missouri, Columbia, MO 65211; e-mail: guyetter@missouri.edu.

² Research Forester, Missouri Department of Conservation, 1110 S. College Ave., Columbia, MO 65201.

natural disturbance regimes with silvicultural prescriptions to foster native plant and animal species diversity (Loucks 1970). Unfortunately, there is little quantitative knowledge about the scale, frequency, and spatial distribution of historic forest disturbance regimes and their legacy on the forest ecosystems of the Ozark Highlands.

The primary objective of this research is to quantify long-term forest disturbance regimes in the Current River Hills Subsection (Nigh *et al.* 2000) of the Ozark Highlands and to relate them to forest succession and plant and animal species associations at the MOFEP study sites. Specific objectives are to 1) quantify disturbance legacy using abrupt growth reductions in shortleaf pine, fire frequency based on a model by Guyette and Dey (2000), historical forest density, and historical grazing protection; 2) relate disturbance legacy to plant successional states; and 3) identify interrelations between disturbance legacy, successional state, and present-day plant and animal species abundance. The central hypothesis is that anthropogenic disturbance and topography have been major factors affecting disturbance frequency at the MOFEP sites and that historic disturbance regimes have a legacy that continues to affect contemporary plant and animal distributions today. Specifically, the roughness of the topography around a site mitigates the propagation of disturbance related factors (fire and logging) and increases the abundance of late-successional plant and animal species.

METHODS

The MOFEP study is described by Brookshire and Hauser 1993, Brookshire *et al.* 1997, and Kurzejeski *et al.* 1993. MOFEP experimental design is described by Sheriff and He (1997) and experimental treatments are described by Brookshire *et al.* (1997).

Quantifying Disturbance

We quantified four measures of disturbance for our analysis: shortleaf pine abrupt growth reduction intervals, mean fire intervals, an 1820 forest "openness" index, and a grazing protection index. Shortleaf pine abrupt growth reduction intervals were estimated using ring-width measurements of 14,801 annual rings from 98 trees on MOFEP sites. Abrupt growth reductions are defined as sudden ring-width reductions that are at least 15 percent of previous growth and that last for 7 or more years. Abrupt growth reduction return intervals are calculated as the number of growth reductions per years of tree growth. The years of record (number of years of growth) for each site (table 1) are the sum of the number of annual growth rings measured on each study site tree. The degree of each growth reduction was calculated by dividing the mean ring-width during the growth reduction by the mean ring-width before the growth reduction and multiplying by 100.

Table 1.—Data and statistics (means and standard deviations) that describe the frequency, degree, and duration of abrupt radial growth reductions in shortleaf pine. Standard deviations are given in parentheses.

MOFEP site number	Number trees	Years of record	Number growth reductions ^a	Reduction return interval (yrs)	Reduction degree (% growth)	Reduction duration (yrs)
1	5	855	2	427	62 (11)	11 (3)
2	13	1,960	6	327	53 (12)	20 (16)
3	13	2,174	8	272	52 (20)	19 (8)
4	9	1,318	4	329	50 (16)	16 (9)
6	9	1,137	5	227	41 (8)	25 (16)
7	11	1,785	21	85	58 (15)	26 (18)
8	4	596	7	85	52 (17)	16 (8)
9	11	1,619	8	202	57 (12)	24 (24)

^a Abrupt growth reductions are sudden ring-width reductions that are at least 15 percent of previous growth for at least 7 years.



Mean fire frequency was estimated with regressions developed from fire scar chronologies at 26 sites in the Current River watershed (Guyette and Cutter 1997, Guyette and Dey 2000) and fire frequency data derived from the MOFEP sites. Regression predictions of fire frequency are used since they are derived from a much larger set of data (26 sites) and a larger range of conditions than individual MOFEP site fire histories, some of which have limited fire scar data or are as yet incomplete. The regression used to predict past fire frequency at the MOFEP sites for this study is:

$$MFI = -442.1 + (449.9 \times topo) - (0.001 \times pop), \quad (1)$$

where: MFI = mean fire interval,
 topo = index of topographic roughness for a 5-km radius circle,
 pop = natural log of human population density times distance upstream,
 n = 78 (three time periods, 29 sites),
 R² = 0.51, variable and intercept significant at P<0.01.

All MFI estimates in this study are for the period of maximum variation in fire frequency between sites, which occurred during three early periods (1700-1780, 1781-1820, 1821-1850). Site-specific fire data from eight of the MOFEP sites are used to show topographic and fire frequency relationships at the MOFEP sites and in the correlation analysis with topographic roughness.

An index of forest openness in 1820—Openness Index (1820)—was constructed as a proxy for the frequency of disturbances that delayed forest succession at the MOFEP sites before European settlement. The index is based upon data compiled from Public Land Survey notes (Batek *et al.* 1999). The index uses two variables: the distance class to bearing trees and the number of survey lines described as open or with few trees. We normalized (divided by the mean) and averaged these variables to develop this index.

We estimated protection from disturbances caused by domestic livestock by calculating the percent of each MOFEP site that has been fenced. The length of fenced portion of the site perimeter was divided by the length of the total site perimeter and multiplied by 100. This index is called the Grazing Protection Index.

Topographic Roughness

The highly dissected topography of the Current River watershed has been shown to affect the spread and frequency of fires during periods of low human population density when anthropogenic ignitions were limited in number (Guyette and Dey 2000). Indices of topographic roughness were developed from the surface area measurements at two different scales (Krstansky and Nigh 1998). Land surface area of 30-m squares within circles of 900 and 5,000 m in radius was calculated and then indexed (divided) by the planimetric surface area of circles of 900 and 5,000 m in radius. The ratios of the actual surface area to the planimetric surface area are the indices of Topographic roughness. Thus, high index values mean the topography is hilly. There is about an 87-percent overlap of the 5,000-m radius circles at MOFEP sites that are adjacent to one another and no overlap of 900-m radius circles. Thus, the spatial data are not completely independent for the larger measure (5,000 m) and the p-values of the correlation coefficients may be biased.

Successional Indices

Successional indices for all overstory tree species (Overstory Successional Index) and for oaks (Oak Successional Index) were developed based on the shade tolerance of species. Data for developing these indices are from Kabrick *et al.* 1997. Indices of forest succession were created by summing the number of trees per hectare of shade tolerant (tolerant to intermediate), late-successional species and subtracting the numbers of trees per hectare of shade intolerant (intolerant to very intolerant), early-successional species (table 2). Many characteristics such as fire tolerance, seed size, and life history might be used to classify tree species into early- and late-successional classes, but are very difficult to quantify. Information on shade tolerance is both available (Abrams 1998, Burns and Honkala 1990, Kramer and Kozlowski 1979) and unbiased (at least with respect to this study), and shade tolerance is important in the succession of plant species under conditions of changing light levels. In addition, shade tolerance is inversely related to the compensation points and dark respiration among tree species. Shade intolerant species show the greatest plasticity in growth response

Table 2.—Successional indices based on the shade tolerance (Burns and Honkala 1990) of overstory tree species are the number of early-successional (right side of table) individuals (trees > 11.4 cm) subtracted from the number of late-successional individuals (left side of table).

OAK SUCCESSIONAL INDEX			
LATE SUCCESSION		EARLY SUCCESSION	
Species	Shade tolerance	Species	Shade tolerance
<i>Q. alba</i>	intermediate	<i>Q. coccinea</i>	very intolerant
<i>Q. rubra</i>	intermediate	<i>Q. stellata</i>	intolerant
<i>Q. velutina</i>	intermediate	<i>Q. marilandica</i>	intolerant

OVERSTORY SUCCESSIONAL INDEX (oaks+others)			
LATE SUCCESSION		EARLY SUCCESSION	
<i>Acer saccharum</i>	very tolerant	<i>Juniperus virginiana</i>	very intolerant
<i>Acer rubrum</i>	tolerant	<i>Pinus echinata</i>	intolerant
<i>Carya glabra</i>	intermediate	<i>Carya tomentosa</i>	intolerant
<i>Nyssa sylvatica</i>	tolerant	<i>Carya texana</i>	intolerant

to light (Kozlowski *et al.* 1991). Thus, because of their higher potential growth rates, shade intolerant species are more adaptive to early-successional stages in high disturbance environments. Competitive exclusion, reproductive strategies, and size-related fire effects on mortality favor their numbers during early-successional stages.

The Seedling Successional Index was developed for tree species under 1 m in height, using the data of Grabner *et al.* (1997). The frequency of plots with shade tolerant (and intermediate) versus shade intolerant tree species was differenced by subtraction. The sum of the number of plots at each MOFEP site that had shade intolerant species (*Quercus stellata*, *Quercus marilandica*, *Ulmus alata*) was subtracted from the sum of the number of plots with shade tolerant species (*Acer saccharum*, *Carya glabra*, *Ulmus rubra*, *Viburnum rufidulum*) to develop the Seedling Successional Index.

Many factors associated with disturbance, succession, and fire may affect the ecology and distribution of *Armillaria* spp. (Kile *et al.* 1991). We hypothesize that the spatial distributions of long-lived species such as *Armillaria* spp. (Bruhn *et al.* 2000) may reflect their adaptations for different host tree species, for live or dead woody substrate, and for certain fire effects, such as the removal of woody debris by burn-

ing. An *Armillaria* successional index was constructed by subtracting the percent of sites where *Armillaria mellea* was detected from the percent of sites where *Armillaria gallica* was detected. *Armillaria* data from Bruhn *et al.* (1997) were used to calculate the *Armillaria* Successional Index for the MOFEP sites.

Composite Successional Indices were constructed from MOFEP data based on normalized values of disturbance and species variables. Two composite indices were developed based on disturbance variables, species abundances, and characteristics. All variables were scaled so that the highest index values indicated the most advanced successional stages or had the longest mean disturbance-free interval. These indices are relative values with a mean of one. The disturbance-free interval index was calculated as the mean of normalized growth reduction return intervals, the normalized fire return intervals, the standardized protection from open range grazing, and standardized Government Land Office note data on forest openness (Batek *et al.* 1999). The Species Successional Index was calculated as the mean of the standardized values of the Overstory Successional Index, the Seedling Successional Index, the *Armillaria* spp. Successional Index, a standardized measure of five forest bird species nesting territories, a standardized measure of the abundance of five lizard species, and standardized blueberry fruit abundance.



Species Associations

Two years of blueberry abundance data at the study plots (Fantz and Hamilton 1997) were used to illustrate the effects of disturbance and succession on soft mass. Low bush blueberry (*Vaccinium vacillans*) data were used because of the abundance of this species across sites and the lack of an association between the abundance of this species and sitewide substrate.

Data of Clawson *et al.* (1997) on the abundances of five forest dwelling bird species (ovenbird, *Seriurus aurocapillus*; worm-eating warbler, *Helmitheros vermivorus*; Kentucky warbler, *Oporornis formosus*; wood thrush, *Hylocichla mustelina*; Acadian flycatcher, *Empidonax virescens*) were used in the correlation analysis. The total number of nesting territories of the five birds species was also used in the correlation analysis.

Data on reptile and amphibian captures from Renken (1997) were used in the correlation analysis. The total numbers of captures of four skinks (broadhead skink, *Eumeces laticeps*; coal skink, *Eumeces anthracinus*; five-lined skink, *Eumeces fasciatus*; ground skink, *Scincella lateralis*) and one lizard species (fence lizard, *Sceloporus undulatus*) commonly found at the MOFEP sites were also used in the correlation analysis.

Genetic data on the inbreeding of two tree species (*Quercus alba*, *Sassafras albidum*) was used in the correlation analysis (Sork *et al.* 1997). We include data on these tree species and our analysis of them based on the hypothesis presented by these authors, that differences in genetic inbreeding and diversity may be related to the environmental history of the MOFEP sites.

Statistical Analyses

Correlation analysis was used to evaluate relationships among disturbance variables, successional indices, and plant and animal abundances. Correlation coefficients and their corresponding significance levels were calculated using SAS programming and statistical procedures (SAS 1989). We used site-level data, so all correlations and associations have a maximum of nine observations. The small sample size made it impossible to determine if variables were normally distributed, which is a

requirement for hypothesis testing in correlation analysis. Therefore, caution is needed when interpreting significance of correlations. Despite this limitation, the correlation analysis has strength in its simplicity for evaluating associations among many diverse variables measured in many different ways.

Independence of observations is also a requirement of hypothesis testing. Significance levels in correlation analysis can be biased when observations of a population are statistically dependent in space or time. Spatial and serial data are often autocorrelated. We examined the autocorrelation function of the Species Successional Index to assess the independence of our variables. We used the Species Successional Index because this index incorporates many species, it is at the heart of our general hypothesis, and its use would overcome many of the problems involved in estimating autocorrelation functions for individual species from data sets with few observations at the regional level. An autocorrelation function was calculated by correlating the distance between all possible pairs of MOFEP sites with the difference between the index values at each site pair. Correlations were calculated for five distance classes of 4.8 km (3 mi) each. The autocorrelation functions for the Species Successional indices showed no significant autocorrelation at any of the five distance lags. A function of diminishing correlation with distance, which was expected, was not found. The lack of significance and pattern in the spatial autocorrelation function indicates that observations are independent and that most of the data and significance levels are unbiased. If there is an underlying population autocorrelation function, it was not apparent in the sample data. The lack of significant autocorrelation may in part be due to the small number of site comparisons (36) and their distribution with distance. However, even when we grouped distance into two classes (<12, >12 km), there was no significant correlation among single variable differences and distance between sites.

We performed several analyses on a studywide basis. The first was to compare the number of significant versus the number of non-significant correlations we found to the number of significant and non-significant correlations that would be expected by chance alone. Significance for this test was based on the rejection of the null hypothesis for tests of individual biological hypotheses. The 38 significance levels of the

correlations for all individual species with the Disturbance Interval Index (made up of non-species data) were classed ($p < 0.05$, $p < 0.1$, non-significant) and counted. The percentages of significant versus non-significant correlations were calculated and compared with the percentage of significant correlations that would be expected by chance alone. The second test was a sequential Bonferroni test (Rice 1989, Holm 1979) designed for simultaneous testing of a number of variables. This test was performed on the correlation matrix among 11 disturbance, successional, and species groups (table 4) to adjust for the increased probability of not

rejecting a true null hypothesis when a number of variables are tested simultaneously. Third, a group (table 3) of several correlations addressing the same question (is topographic roughness associated with all disturbance and species variables as a group) was evaluated as a common null hypothesis by the use of canonical correlation analysis and CANCORR statistical software (SAS 1989). Variables were combined by averaging into two groups, historic and current (table 3), to use measurements of both the present and past conditions at the sites and to increase the degrees of freedom in the canonical correlation analysis.

Table 3.—Correlation coefficients among topographic roughness and disturbance variables, successional indices, fruit production, species abundances, and inbreeding at the MOFEP sites. This table illustrates the numerous associations of topographic roughness with many very different, but disturbance-related variables within the ecosystem. P-values are given in parentheses for tests of individual hypotheses. Simultaneous hypothesis testing with a sequential Bonferroni (Rice 1988) test yields no significant ($\alpha = 0.05$) correlations for variables in the first 11 rows. Emphasis is placed, however, on the significance level of the multivariate analysis of canonical variables (see text) with topographic roughness (last row) for the nine MOFEP sites. This analysis correlates all variables (first 11 rows) in two groups (first column) with topographic roughness at two scales.

Group	Variable	Topographic Roughness Index ^a (900 m radius)	Topographic Roughness Index (5,000 m radius)
Historic	Growth reduction interval	0.70 (0.03)	0.86 (0.01)
Historic	Mean fire interval (1700-1850)	0.43 (0.25)	0.80 (0.01)
Historic	Openness Index (1820) ^b	-0.72 (0.03)	-0.79 (0.01)
Historic	Overstory Succession (1820)	0.59 (0.10)	0.66 (0.05)
Current	Overstory Successional Index ^c	0.77 (0.02)	0.81 (0.01)
Current	Seedling Successional Index ^d	0.77 (0.02)	0.76 (0.02)
Current	<i>Armillaria</i> Successional Index ^e	0.57 (0.11)	0.53 (0.14)
Current	Blueberry fruit density ^f	-0.68 (0.04)	-0.79 (0.01)
Current	Forest bird territories ^g	0.52 (0.15)	0.48 (0.18)
Current	Lizards ^h	-0.43 (0.25)	-0.54 (0.14)
Current	Sassafras inbreeding ⁱ	-0.51 (0.16)	-0.74 (0.02)
All	Canonical variables (2 groups)	0.82 (0.04)	0.85 (0.02)

^a Data: Krstansky and Nigh (1999).

^b Batek *et al.* (1999).

^c Data: Kabrick *et al.* (1997).

^d Data: Grabner *et al.* (1997).

^e Data: Bruhn *et al.* (1997).

^f Fantz and Hamilton (1997).

^g Data: Clawson *et al.* (1997).

^h Data: Renken (1997).

ⁱ Data: Sork *et al.* (1997).



Table 4.—Correlation coefficients for disturbance, successional, and species variables for the nine MOFEP sites. Significance levels for individual hypothesis testing ($\alpha < 0.05$) are in parentheses while those for simultaneous hypothesis testing (Rice 1989) at $\alpha < 0.05$ are denoted by an *.

	Mean fire interval	Openness Index (1820) ^a	Overstory Index (1820)	Overstory Succession Index ^b	Seedling Succession Index ^c	<i>Armillaria</i> Succession Index ^d	Blueberry fruit density ^e	Forest bird territories ^f	Skink and lizard captures ^g	Sagebrush Inbreeding ^h
Mean abrupt growth reduction interval	0.98* (0.0001)	-0.82 (0.001)	0.82 (0.006)	0.71 (0.05)	0.83 (0.01)	0.77 (0.016)	-0.83 (0.005)	0.64 (0.07)	-0.67 (0.05)	-0.1 (0.1)
Mean fire interval		-0.86 (0.003)	0.79 (0.01)	0.77 (0.02)	0.83 (0.01)	0.72 (0.023)	-0.84 (0.004)	0.68 (0.047)	-0.68 (0.04)	-0.1 (0.1)
Openness Index (1820)			-0.85 (0.004)	-0.85 (0.006)	-0.87 (0.002)	-0.78 (0.01)	0.94* (0.0003)	-0.80 (0.01)	0.57 (0.11)	0.4 (0.1)
Overstory Succession Index (1820)				0.76 (0.02)	0.92* (0.0005)	0.93* (0.0003)	-0.87 (0.002)	0.92* (0.0005)	-0.80 (0.01)	-0.1 (0.1)
Overstory Succession Index					0.93* (0.0003)	0.74 (0.02)	-0.71 (0.032)	0.76 (0.009)	-0.59 (0.10)	-0.1 (0.1)
Seedling Succession Index						0.92* (0.0004)	-0.82 (0.007)	0.92* (0.0004)	-0.73 (0.03)	-0.1 (0.1)
<i>Armillaria</i> Successional Index							-0.76 (0.018)	0.97* (0.0001)	-0.77 (0.01)	-0.1 (0.1)
Blueberry fruit density								-0.78 (0.013)	0.57 (0.112)	0.4 (0.1)
Forest bird territories									-0.65 (0.056)	-0.1 (0.1)
Skink and lizard captures										0.7 (0.1)

^a Batek *et al.* 1999.
^b Kabrick *et al.* 1997.
^c Grabner *et al.* 1997.
^d Bruhn *et al.* 1997.
^e Fantz *et al.* 1997.
^f Clawson *et al.* 1997.
^g Renken 1997.
^h Sork *et al.* 1997.

RESULTS

Topographic Roughness and Disturbance

Many of the disturbance variables and indices were highly associated with topographic roughness (table 3) and indicate that increasing topographic roughness around a site decreases the frequency of disturbance. Canonical correlation analysis of the two groups of 11 variables (historic versus current variables, table 3) with topographic roughness showed significant correlation between topographic roughness and the canonical variable for the two groups. The mean fire interval (modeled with topographic roughness), the growth reduction return intervals, and the Openness Index (1820) were all significantly correlated with each other (table 4). Significant correlations among topographic roughness, growth reductions, fire frequency, and other measures of disturbance suggest that topographic roughness is a strong factor mitigating the frequency of disturbance and fire.

Disturbance, Successional Indices, and Species Associations

Tests of the significance of correlations on a studywide basis yielded results that indicate the rate of significant correlation among study variables is much more than would be expected by chance alone. Significant correlations among individual species and the Disturbance Interval Index occurred eight times more often than is expected by chance alone at the 0.05 level and five times more often than expected by chance at the 0.1 level (table 5). A sequential Bonferonni analysis, based on the assumption of simultaneous testing as opposed to the

testing of individual, ecologically generated, hypotheses, yielded nine significant correlations from the correlation matrix (table 4).

Study site means of abrupt growth reductions ranged from 41 to 62 percent and had mean durations that ranged from 11 to 26 years (table 1). Growth reduction return intervals in shortleaf pine were significantly correlated with many variables (table 4), such as fire frequency, the Overstory Successional Index, the Oak Successional Index, the Seedling Successional Index, inbreeding coefficients of sassafras (Sork *et al.* 1997), and the sign of correlation was consistent ecology theory. Specifically, early successional species were more abundant at sites where pines had short mean growth reduction intervals while late successional species were more abundant at sites with long mean growth reduction intervals.

The frequency of historic growth reductions in shortleaf pine was significantly correlated with the abundance of several wildlife species. The combined density of five forest birds territories was correlated with growth reduction return intervals (table 4). The historic (1700-1850) mean fire intervals were correlated with the modern frequency of two (worm-eating warbler (*Helmitheros vermivorus*), $r=0.75$, $p=0.02$; Acadian flycatcher (*Empidonax virescens*), $r=0.85$, $p=0.004$) of five forest bird population densities measured by Clawson *et al.* (1997). The frequency of historic growth reductions in shortleaf pine was significantly correlated (table 4) with the sum of the abundance estimates of five lizards (*Eumeces laticeps*, *Eumeces anthracinus*, *Sceloporus undulatus*, *Eumeces fasciatus*, *Scincella lateralis*) measured at the MOFEP sites by Renken (1997). The broad

Table 5.—The number and percent of individual species variables that are significantly and non-significantly correlated with the Disturbance Interval Index at two levels of probability. Percent values are given in parentheses.

	Significant correlations with disturbance	Non-significant correlations with disturbance	Total number of species correlations	Significant correlations expected by chance alone
Number correlations ($\alpha = 0.05$)	16 (42%)	22 (58%)	38 (100%)	1.9 (5%)
Number correlations ($\alpha = 0.10$)	20 (53%)	18 (47%)	38 (100%)	3.8 (10%)



headed skink was the lizard species most highly correlated ($r=0.74$, $p=0.02$) with the growth reduction return intervals. The historic (1700-1850) mean fire intervals were also significantly correlated with the present-day abundance estimates of the sum of five lizards. Two reptile species, the copperhead (*Agkistrodon contortrix*) and the three-toed box turtle (*Terrapene carolina*), were correlated ($r=0.75$, $p=0.02$; $r=0.77$, $p=0.01$) with growth reduction return intervals. No amphibians (*Notophthalmus viridescens*, *Ambystoma opacum*, *Plethodon serratus*, *Plethodon glutinosus*, *Ambystoma maculatum*, *Bufo americanus*, *Rana clamitans*, *Rana palustris*, *Rana utricularia*, *Pseudacris crucifer*) were significantly correlated with growth reduction intervals.

Successional indices, based on the shade tolerance of tree species were related to a number of variables in addition to their correlation with growth reduction variables. Two of the succession indices (Overstory Tree Species and Oak) are not independent, however, since the same oaks comprise the majority of the number of individual trees counted in both indices. Successional indices of both oak and all overstory species were highly correlated with the mean fire interval (fig. 1) at the nine MOFEP sites. A significant correlation was found among the mean number of tree species per plot at the MOFEP sites and the Overstory Successional Index ($r=0.68$, $p=0.04$). The Oak Successional Index, although not significantly correlated ($r=0.56$, $p=0.11$) with the number of tree species per plot, had a similar pattern. The Seedling Succession Index, made up of sugar maple, winged elm, slippery elm, black haw, post oak, and blackjack oak was significantly correlated with the Oak and Overstory Tree Species successional indices.

Successional indices were correlated with both forest birds and lizards (table 4). Successional indices were significantly correlated with the sum of five forest bird territories and strongly correlated with the number of territories of Acadian flycatchers (*Empidonax vireescens*) ($r=0.88$, $p=0.0015$) and worm-eating warblers (*Helmitheros vermivorus*) ($r=0.92$, $p=0.0005$). Not all individual forest bird species were significantly correlated with the Overstory Successional Index. Ovenbirds (*Seiurus aurocapillus*) were not significantly correlated with the all species successional index (0.55, $p=0.12$) but were significantly correlated with

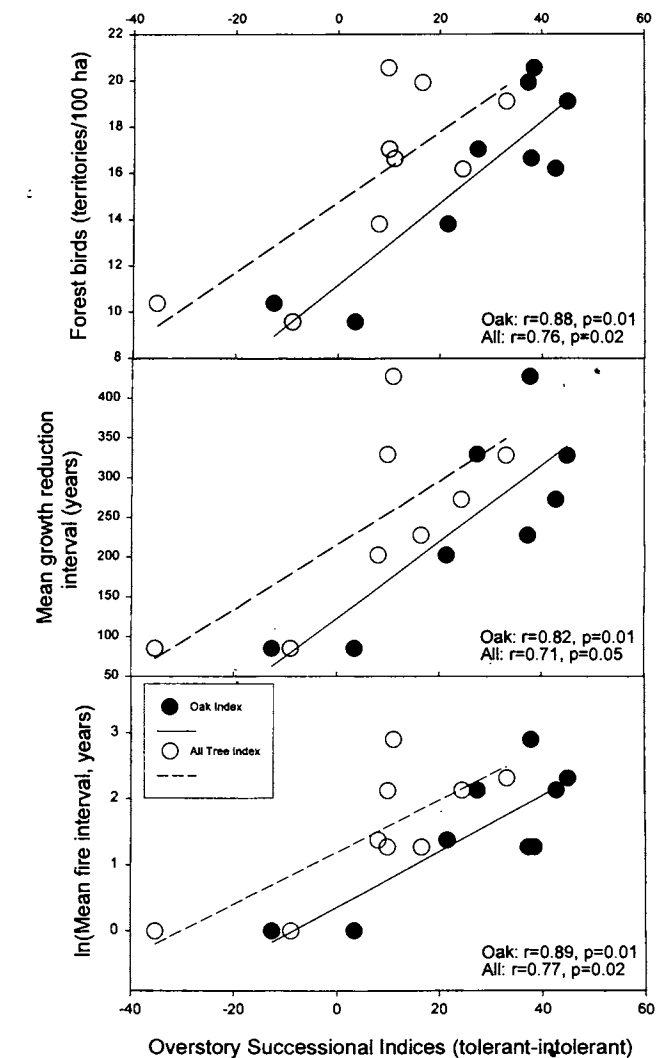


Figure 1.—Relationships between the Overstory Successional Indices (all tree species and oak tree species) and the mean fire return interval, the mean growth reduction return interval, and the density of forest bird territories. The Oak Successional Index is best related to disturbance and species variables. This figure indicates the associations among the successional status of the overstory, disturbance, and species variables.

the Oak Successional Index (0.70, $p=0.04$). Kentucky warblers (*Oporornis formosus*) were not significantly correlated with the all species successional index (0.59, $p=0.10$) or the Oak Successional Index (0.46, $p=0.21$). Wood thrush (*Hylocichla mustelina*) territories were not significantly correlated with the Overstory Successional Index (0.22, $p=0.57$) or the Oak Successional Index (0.38, $p=0.21$). In general,

forest bird species were more highly correlated with the Oak Successional Index than they were with the Overstory Successional Index (fig. 1). All forest bird species were positively correlated with the successional indices.

Successional indices were significantly correlated with the mean number of captures of one lizard (*Sceloporus undulatus*) and four skinks at the MOFEP sites (table 4). Not all lizard species were significantly correlated with the successional indices. The coal skink was most highly correlated ($r=-0.71$, $p<0.03$) with the three successional indices, while the broad headed skink had the lowest correlations ($r=0.45$, $p<0.25$) with the successional indices. All lizard species were negatively correlated with all the successional indices (table 4). Snakes and the three-toed box turtle (*Agkistrodon contortrix*, *Storeria occipitomaculata*, *Diadophis punctatus*, *Terrapene carolina*) were generally positively but not significantly correlated with the successional indices. No amphibians (*Notophthalmus viridescens*, *Ambystoma opacum*, *Plethodon serratus*, *Plethodon glutinosus*, *Ambystoma maculatum*, *Bufo americanus*, *Rana clamitans*, *Rana palustris*, *Rana utricularia*, *Pseudacris crucifer*) were significantly correlated with any of the successional indices.

The abundance of *Armillaria* species was significantly correlated (table 4) with indices of disturbance, species abundance, and succession. *Armillaria gallica* abundance was significant and positively correlated with the time between disturbance events such as the mean fire interval ($r=0.76$, $p=0.02$) and growth reduction return interval ($r=0.81$, $p=0.01$). Forest bird nesting territories ($r=0.96$, $p=0.001$) and all successional indices ($r=0.71$ to 0.91) were also highly correlated with the abundance of *Armillaria gallica*. In contrast, *Armillaria mellea* was negatively correlated with the length of disturbance intervals, successional indices, and forest bird territories ($r=-0.71$, $p=0.03$). Thus, *A. mellea* was more abundant on sites with a high frequency of disturbance while *A. gallica* was less abundant. In contrast, *A. gallica* was more abundant on late-successional sites with less frequent disturbances than was *A. mellea*. The *Armillaria* Successional Index, which incorporated the ratio of the *Armillaria* species (*A. gallica*/*A. mellea*), was positively correlated with disturbance, successional, and species indices (table 4).

The density of blueberry fruit on the MOFEP sites was highly correlated with disturbance variables, successional indices, and species abundances (table 4). Fire frequency and growth reduction return intervals were significantly correlated with blueberry abundance. Successional indices of *Armillaria* species, tree species, oak species, and tree seedlings were significantly correlated with the density of blueberry fruit. Species and species groups that were significantly correlated with blueberry fruit abundance were *Armillaria gallica*, forest birds, lizards, and skinks.

The inbreeding coefficients of sassafras were significantly correlated with the mean fire interval, the growth reduction return interval, and the combined abundance of skink and lizard captures but not significantly correlated with the seven other variables in the correlation matrix (table 4). The inbreeding coefficients of white oak were not significantly correlated with any of the variables in table 4.

Composite Disturbance and Successional Indices

Composite index values were constructed from disturbance variables and species variables (table 6). The Disturbance Interval Index reflects the relative duration between disturbances at each MOFEP site. The Species Successional Index reflects the abundance and successional characteristics of 30 species (10 animal and 20 plant). The Species Successional and Disturbance Interval Indices are significantly correlated ($r=0.89$, $p=0.001$). A logarithmic transformation of the Disturbance Interval Index improved the strength of this relationship ($r=0.93$, $p=0.001$). The Disturbance Interval Index is composed of measurements that are unconstrained by species abundances. On the other hand, the Species Successional Index is based solely on measurements and successional configurations of species abundances. These indices may be of future use in evaluating different types of variables and the responses to MOFEP treatments.



Table 6.—Two indices derived from MOFEP site data that are based on disturbance variables, species characteristics, and abundances. The highest index values indicate the most advanced successional stages or have had the longest mean disturbance interval. The indices are relative values with a mean of one. The Disturbance Interval Index is derived from four disturbance indicators: growth reduction frequency, fire frequency, grazing protection, and pre-European forest structure. The Species Successional Index is derived from standardized values of the Overstory Successional Index, the Seedling Successional Index, the *Armillaria* spp. Successional Index, forest bird nesting territories, lizard abundance, and blueberry fruit abundance.

	Disturbance Interval Index (physical Indicators)	Species Successional Index (species indicators)
SITE 1	1.24	1.14
SITE 2	1.04	1.30
SITE 3	0.95	1.16
SITE 4	1.01	1.19
SITE 5	0.76	1.18
SITE 6	1.12	1.17
SITE 7	0.20	0.47
SITE 8	0.25	0.53
SITE 9	0.77	0.87

DISCUSSION

Disturbance and Topographic Roughness

There is little inherent evidence that accompanies most individual growth reductions in pine trees to indicate the cause. The strength of correlation between growth reduction variables and fire frequency (table 4) indicates that fire is probably the most important cause of most abrupt growth reductions. Some growth reductions begin in the same year that a fire scar is formed or in a year when other trees at a site show fire scars. Many growth reductions, however, are not associated with fire scars and are often found on trees with no fire scars. Growth reductions could include a number of disturbances that affect the growth of shortleaf pine trees such as weather (drought, wind, ice),

insects, *Armillaria* spp., or other pathogens. The inverse relationship between topographic roughness and growth reductions may in part be explained by the impediments to the spread of fire caused by topographic roughness.

Evidence suggests that most growth reductions in shortleaf pine are the result not of low intensity surface fires, but moderate to high intensity wildfires occurring during extreme fire weather, and thus, represent much more severe disturbances that have been recorded on rare survivor trees. Several lines of reasoning point to more severe disturbances as the cause of most growth reductions. The first is that fire intensity and size are exponentially related to frequency (Guyette 1995). Thus, it is reasonable to consider that with an exponential distribution, a mean fire interval of approximately 5 years, and a growth reduction return interval of 85 years, 1 out of every 17 fires might be expected to result in the crown scorch (and a mean radial growth reduction of about 52 percent) of even mature shortleaf pine. The sample trees used to reconstruct growth reduction intervals had an average age of more than 152 years. The average age of a pine tree when a reduction occurred was more than 85 years. Thus, growth reductions were occurring in mature trees with foliage well off the forest floor. Second, since we can only sample what were survivor trees, our estimation of the severity of fires is biased by trees that survived low and high intensity fires. Third, the degree of drought in years in which abrupt growth reductions began indicates severe rather than low intensity fires. Growth reduction events occurred in years with an average Palmer Hydrologic Drought Index value (PHDI=-1.32). That value was well below normal between 1700 and 1850 (Cleavland and Stahle 1997). At least 10 extensive fires occurred in the Current River watershed during years of extreme drought (Guyette 1995) in the 1700s indicating that intense fire, if not common, probably did follow an exponential distribution based on very frequent fires. Fourth, stand replacement events have been documented from pith dates at several sites in the Ozarks (Cutter and Guyette 1994, Guyette 1993). In short, it is difficult to imagine a drought prone ecosystem with abundant anthropogenic ignitions such as in the Ozarks (Guyette and Cutter 1997), in which intense fires occurred less frequently than growth reduction return intervals reported in table 1.

The strong negative correlations between the Openness Index (1820) and growth reduction interval, mean fire frequency, and topographic roughness suggest that fire, mitigated by local topography, played a primary role in reducing the density of the pre-European forest. This is consistent with the findings of Batek *et al.* (1999), who show for Missouri's Current River region that areas of greater tree densities, as determined from witness tree distances in Public Land Survey notes, were found where the landscape is more dissected. Areas having low topographic roughness (i.e., less dissection) have fewer natural fire breaks and consequently have a greater fire frequency and/or greater fire intensity than areas having greater topographic roughness.

The effects of topographic roughness on the ecosystems of the Current River watershed have not been limited to fire-related disturbances. Topographic roughness has been and still is an important factor affecting anthropogenic disturbances to forested environments. Logging and transportation have always been inhibited by high degrees of topographic roughness. For example, remnants of intense logging disturbance are much greater at MOFEP sites 7 and 8 than at the other MOFEP sites. Clearcutting of these sites in about 1900 is evident from the fact that few, if any, trees on these sites are older than 100 years. Clearcutting here was made economical by the much gentler slopes and valleys of these sites. MOFEP sites high in topographic roughness such as sites 3 and 4 show evidence, via their tree-age structure, of being selectively logged over a period of many years. In general, the relationship of topographic roughness to disturbance is that the effects of any phenomena propagated via the land surface will be mitigated by topographic roughness. This would include such diverse phenomena as wildland fire, logging tracks, grazing, road construction, seed dispersal, and aquatic and terrestrial species movements. Table 3 suggests that in addition to the associations of vegetation with the soils and geology (Meinert *et al.* 1997), topographic roughness and successional sequences should be considered in characterizing biotic associations.

Disturbance, Succession, and Species Associations

The significant correlations among disturbance measures, successional indices, and species associations support our central hypothesis that historic disturbance regimes have a legacy that is apparent in contemporary plant and animal distributions at MOFEP sites. The tree species successional indices are one dimensional in nature, that is, based only on shade tolerance and not on the fire-related characteristics of each species. Despite some inherent limitations, these indices indicate autogenic succession in a forest ecosystem in which shade intolerant species are replaced by shade tolerant species as a growth limiting factor (light) changes.

A recent study that reconstructs early 19th century vegetation (Batek *et al.* 1999) supports the hypothesis that fire-related disturbances had a strong effect on tree species distributions over a much broader range in the Current River watershed than the range of the MOFEP study sites. The spatial distribution of shortleaf pine, red oaks, eastern redcedar, sugar maple, and red maple in 1820 is related to the frequency of fire reconstructed from fire scar chronologies.

Armillaria spp. are long lived (Bruhn *et al.* 2000) and as such may persist in the continuum of a long-term disturbance regime. Differences in the abundance and pathogenicity of *Armillaria* species may be linked to factors such as the abundance of woody debris and the frequency of tree stress (Kile *et al.* 1991). These factors are mitigated and controlled by fire frequency and succession. We propose the hypothesis that *Armillaria* species at the study sites are distributed with respect to disturbance regimes created by the long-term effects of fire and logging and the subsequent patterns of forest succession.

The abundance of blueberry fruit at the MOFEP sites lies along a successional gradient as indicated by its correlation with successional indices. This is true even though the occurrence of blueberry plants is not significantly correlated with any of the successional indices or disturbance variables. The abundance of blueberry fruit probably reflects more light energy near the ground surface at early-successional sites.

If the successional indices indicate a degree of forest succession at the MOFEP sites, then it follows that there might be an observable relationship between species diversity and successional stage. This is perhaps the most interesting corollary and prediction of our hypothesis that the long-term interactions of fire, topography, and anthropogenic disturbance have resulted in a successional gradient among the MOFEP sites. Thus, succession, in addition to soils, substrates, and land forms, may be a factor controlling species diversity within forest successional stages. Until the development of the successional indices presented here, judgments about Ozark forest succession were largely qualitative. The successional indices allow for the quantitative testing of successional corollaries. Herein lies an important new tool for understanding ecosystem dynamics in the Ozarks.

There are many theories concerning how diversity changes within a successional sere (Hunter 1990, Loucks 1970), but data on diversity and the succession of macrospecies suggest that mid-successional stages have the highest species diversity because these transitional stages have species adapted to both early- and late-successional stages (Loucks 1970). On the other hand, early- and late-successional stages have the least diversity because of the limitations imposed by vegetation and the physical environment. At the MOFEP sites, the mean number of overstory tree species is significantly correlated with the Overstory Successional Index. The linear relationship between the Overstory Successional Index and the number of tree species per plot can be interpreted in at least two ways. One interpretation is that species diversity reaches its peak during late-successional stages (Odum 1969) at the MOFEP sites. A second interpretation is that peak diversity is reached at mid-successional stages but that none of the forests at the study sites have reached late-successional stages. Both of these interpretations may have merit at the MOFEP sites, but certainly, none of these sites have been free of disturbance (fire and logging) for more than 60 years.

Another indication that diversity is affected by disturbance regimes and succession is the relationship between genetic diversity of a species and disturbance as proposed by Sork *et al.* (1997). These investigators hypothesized that

“the year of acquisition” was a proxy disturbance variable and was related to trends in the inbreeding coefficients of sassafras at the MOFEP sites. The correlation of genetic inbreeding coefficients and disturbance and successional variables (table 4) supports the hypothesis that historic and long-term disturbance regimes may have an effect on genetic diversity of some tree species.

Another corollary of our successional hypothesis is that animal species, which are often adapted to various stages of forest succession, should be distributed along a gradient as quantified by the successional indices. Avian nesting populations have been related to stages of forest succession (Thompson and Dessecker 1997). Forest bird nesting populations at the MOFEP sites, as defined by Clawson *et al.* (1997), are adapted to late-successional forest habitats. In general, the positive relationships between forest bird species and the successional indices support the hypothesis that the forests at the MOFEP sites are in various stages of succession. In contrast to forest bird species, the negative correlations between successional indices, disturbance variables, and (table 4) lizard species indicate that lizard species are in general early-successional species whose abundance diminishes as overstory succession progresses.

Although none of the five salamander species were significantly correlated with any of the disturbance or successional variables or indices, there may be several reasons why this is not an indication that no change in their abundance might occur with a forest disturbance. There could, for example, be spatially limiting factors in their abundance, such as breeding habitat or coarse woody debris, that limit their abundance at the MOFEP sites. Schurbon (2000) found no negative effects of prescribed fire on amphibians but did find that Ambystomid salamanders were more common in forests that had not burned within 3 years. Also, the low power (only nine observations) of the test data may not be enough to detect weaker relationships. For example, the abundance of southern redback salamanders (*Plethodon serratus*) is correlated ($r=0.59$, $p=0.10$) with the length of the growth reduction return intervals, suggesting a possible relationship with disturbance.

Disturbance Frequency and Species Longevity

The strength of correlation between the Disturbance Interval Index and the abundance of tree species was related to their potential longevity (fig. 2). The absolute value of r (for the Disturbance Interval Index versus tree species abundance) was related to the mean maximum longevity of 16 common tree species at the MOFEP sites. This implies that a legacy of the long-term disturbance regime persists on the MOFEP sites to the greatest extent in organisms

that are long lived. This is to be expected since they take up more resources for longer periods, reach reproductive age later, and have longer periods of reproduction. Tree species provide an excellent example of this relationship because of the considerable variability in longevity of different tree species and because the documentation of their ages in both the literature (Burns and Honkala 1990) and in the study region. Tree species longevity accounts for about 73 percent of the variance in the correlation strength (absolute r value) between the Disturbance Interval Index and their abundance

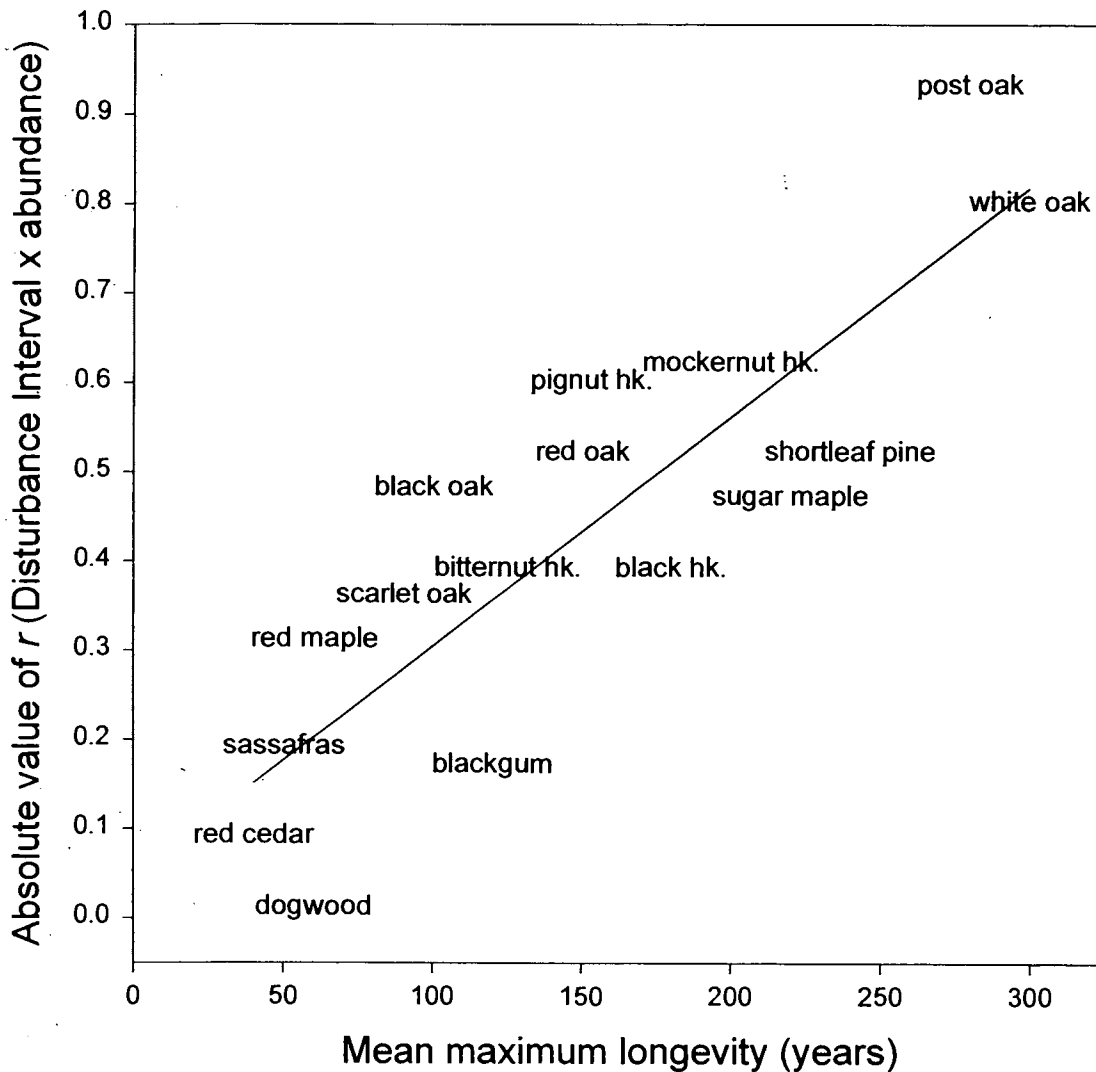


Figure 2.—Long-lived species are more strongly related to differences in long-term disturbance regimes. Tree species longevity accounts for about 73 percent of the variance in the strength of correlation (absolute value of r) between the Disturbance Interval Index and a tree species abundance. For instance, post oak, a long-lived species, is strongly and negatively correlated with a high frequency of disturbance, while white oak, also a long-lived species, is strongly and positively correlated with a low frequency of disturbance. Both these species are thus good indicators of the long-term disturbance frequency. In contrast, the abundance of sassafras, a short-lived species, is weakly correlated with disturbance frequency, high or low.



(fig. 2). Thus, the long-term legacy of disturbance is best reflected on a site by the relative abundance of long-lived species. Another example of the relationship between species longevity and disturbance frequency can be found in the distribution of *Armillaria* spp., which are among the longest lived (Shaw and Kile 1991) species in many forests. Among the different organisms at the study sites, *Armillaria* spp. are one of the most strongly correlated with the disturbance and successional correlation matrix (table 4). In summary, long-lived tree and fungal species have more ecological persistence and best reflect the long-term gradient in ecosystem stability that has occurred at the MOFEP sites.

Implications for MOFEP

Many factors will influence the rate of change at the MOFEP sites in the years to come. The extent to which the frequency of disturbance (treatments) at the MOFEP sites compares with that over the last centuries will be a major factor affecting change. Limited comparisons can be made between historic disturbance regimes and MOFEP treatments using fire history reconstructions (Guyette 1995, Guyette and Cutter 1997, Guyette and Dey 2000). Fire frequency and fire area per year in the Current River watershed can be compared with MOFEP treatments (fig. 3). A treatment with a 10-year re-entry and 10-percent overstory removal is similar to what is reconstructed for the historic fire regime. Not all fires, however, were stand

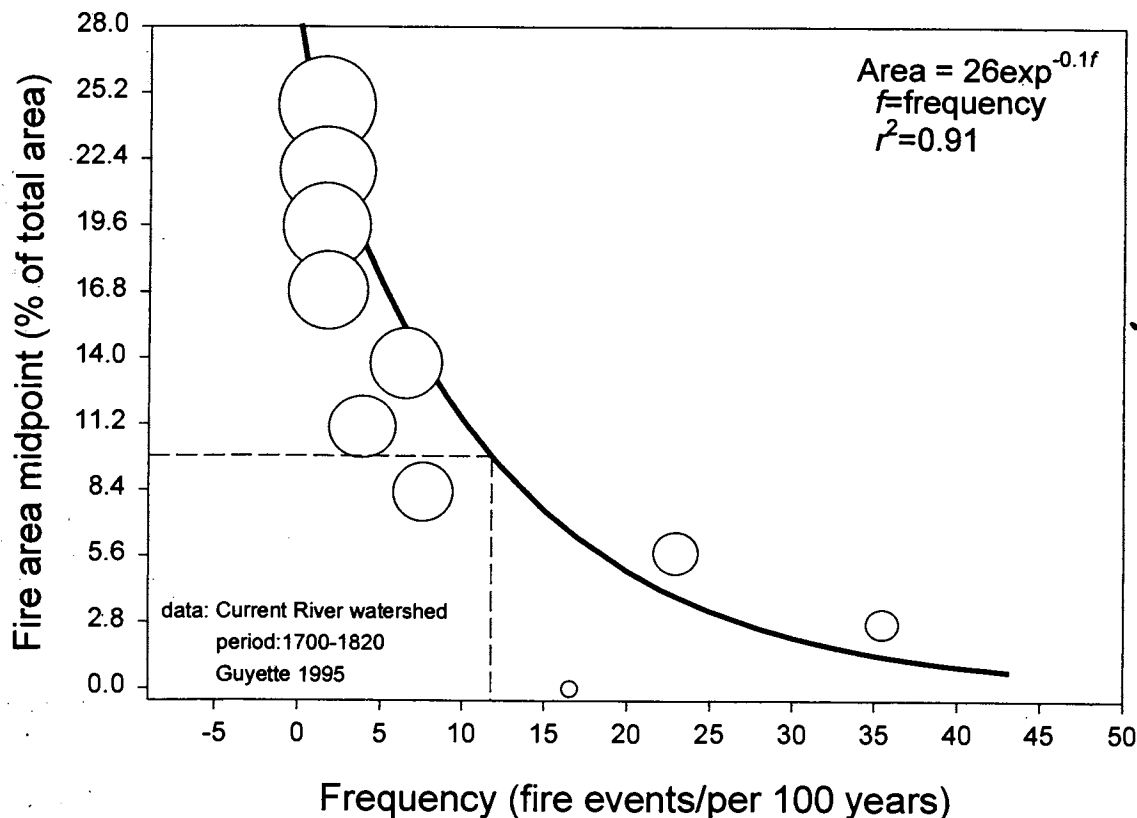


Figure 3.—Relationship between fire frequency and fire area per year in the Current River watershed and how this historic fire regime compares with MOFEP even-aged treatments. The dotted lines represent treatment intervals and areas that approximate MOFEP treatments. The regression line is based on the 10 midpoints and the frequency data. The areas of the circles are roughly proportional to the area class of the midpoint. This figure indicates that the disturbance frequency created by the MOFEP even-aged treatments is similar to the long-term disturbance frequency in the region. This does not imply that even-aged treatments are qualitatively similar to stand replacement by fire.

replacement events. Indeed, the vast majority of fires were low intensity surface fires. Fire intensity and stand replacement were probably much greater for those years in which large areas burned. For example, four large fires (2 largest data points, fig. 3) occurred in 120 years. These events are estimated to have burned up to a quarter million acres in a single year. These fires alone burned an area equivalent to the whole Current River watershed in 120 years. Thus, if 10 percent of the area burned in these fires was of sufficient intensity to initiate stand replacement, then an average of about 12 percent of the forests were replaced every 120 years. Differences in scale and intensity limit the implications of these comparisons, but even-aged treatments and rotations may not differ from historic disturbance regimes.

Our findings provide a means for predicting how MOFEP sites will respond to silvicultural treatments based on the historic and present successional stages of the MOFEP sites and the nature of treatments applied. Species composition is expected to change at both sites with infrequent historical disturbances (high disturbance-free indices) and at sites with frequent historical disturbances (low disturbance-free indices). Even-aged treatments are more likely to enhance early-successional species than uneven-aged treatments. No-harvest treatments will enhance late-successional species. However, these trends will be mitigated by the present status and direction of succession at the sites. Disturbance and species successional indices (table 6) and no-harvest treatment suggest that species abundance and distributions in control sites 1 and 6 will change very little because of their late-successional status and no-harvest treatment. The continued protection from fire at these sites may contribute to limited changes in vegetation, however. Sites 1 and 6 may provide the best late-successional controls. Even-aged site 9 will also change very little because of its early-successional state and even-aged treatment. Site 2 is difficult to predict because of its uneven-aged treatment and mixed index values (table 6). Early-successional stages will be maintained to some degree at MOFEP site 7 by uneven-aged treatments, which will continue to set back the successional development as both natural and anthropogenic disturbances have for centuries. Similarly, early-successional stages will be maintained at site 5 through the use of even-aged treatments. Site 4 will change

more than sites 1, 6, 7, and 9 because of its late-successional state and uneven-aged treatment. Control site 8 will change more than sites 1, 6, 7, 9, and 4 in species abundances and distributions because of its early-successional stage, protection from fire and logging disturbance, and its no-harvest treatment. Finally, site 3 may change the most due to the combined effects of its relatively infrequent historic disturbances and its even-aged treatment.

SUMMARY

A correlation matrix of species distributions and species characteristics support the hypothesis that the interactions of fire, topographic roughness, and disturbance have resulted in varied successional stages among the MOFEP sites. A continuum of anthropogenic disturbance patterns, from wildfire to logging, spans the historic period (1700-1850) and the 20th century. This continuum is caused by the effects of topographic roughness on the propagation of fire and human activities across the landscape. The successional construct offers much in terms of interpreting pre-treatment data at the MOFEP sites and will offer even more in interpreting and predicting MOFEP experimental results. Disturbance frequency and succession have and will continue to change the distribution of species at the MOFEP sites. The successional indices presented here have many potential uses in ecology, forestry, and wildlife management. Biologically based successional indices could be created for other classes and guilds of species and could present new ways of interpreting complex ecological data. A rule of thumb relating topographic roughness to disturbance is that the effects of any phenomena propagated via the land surface will be mitigated by topographic roughness.

ACKNOWLEDGMENTS

The authors thank the Missouri Department of Conservation's Missouri Ozark Forest Ecosystem Project and the taxpayers of Missouri for supporting this effort. The authors also thank all the principal investigators of the MOFEP project for their efforts, consultations, and long hours spent in the diligent collection of these remarkable data.



LITERATURE CITED

- Abrams, M.D. 1998. The red maple paradox. *Bioscience*. 48(5): 355-364.
- Batek, M.J.; Rebertus, A.J.; Schroeder, W.A.; Haithcoat, T.L.; Compas, E.; Guyette, R.P. 1999. Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri Ozarks. *Journal of Biogeography*. 26: 397-412.
- Brookshire, B.L.; Hauser, C.H. 1993. The Missouri Ozark Forest Ecosystem Project: The effects of forest management on the forest ecosystem. In: Gillespie, A.R.; Parker, G.R.; Pope, P.E.; Rink, G.R., eds. Proceedings of the 9th Central hardwood forest conference; 1993 March 8-10; West Lafayette, IN. Gen. Tech. Rep. NC-161. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 289-307.
- Brookshire, B.L.; Shifley, S.R. 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. 378 p.
- Brookshire, B.L.; Jensen, R.G.; Dey, D. 1997. The Missouri Ozark Forest Ecosystem Project: Past, present, and future. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 1-25.
- Bruhn, J.N.; Wetteroff, J.J., Jr.; Mihail, J.D.; Burks, S. 1997. Determination of the ecological and geographic distributions of *Armillaria* species in Missouri Forest ecosystems. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 257-273.
- Bruhn, J.N.; Wetteroff, J.J., Jr.; Mihail, J.D.; Kabrick, J.M.; Pickens, J.B. 2000. Distribution patterns of *Armillaria* species in upland Ozark Mountain forests with respect to site, overstory species composition, and oak decline. *Forest Pathology*. 30: 43-60.
- Burns, R.M.; Honkala, B.H. 1990. Silvics of North America, vol. 2, hardwoods. *Agric. Handb.* 654. Washington, DC: U.S. Department of Agriculture, Forest Service. 877 p.
- Clawson, R.L.; Faaborg, J.; Seon, E. 1997. Effects of selected timber management practices on forest birds in Missouri oak-hickory forests. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 274-288.
- Cleavland, M.K.; Stahle, D.W. 1997. Variability of hydrologic drought in the Ozark Highlands, 1680-1980. In: Dean, J.; Meko, D.; Swetnam, T., eds. Tree rings, environment and humanity: Proceedings of the International Conference; Tucson, AZ: 43-50.
- Cunningham, R.J.; Hauser, C. 1989. The decline of the Ozark forest between 1880 and 1920. In: Waldrop, T.A., ed. Proceedings of pine-hardwood mixtures: A symposium on the management and ecology of the type; 1989 April 18-19; Atlanta, GA. Gen. Tech. Rep. SE-58. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station: 34-37.
- Cutter, B.E.; Guyette, R.P. 1994. Fire history of an oak-hickory ridge top in the Missouri Ozarks. *American Midlands Naturalist*. 132: 393-398.
- Fantz, D.K.; Hamilton, D.A. 1997. Abundance and production of berry-producing plants on the MOFEP study sites: the soft mast study pre-harvest conditions (1994-1995). In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193.

- St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 210-230.
- Galloway, J.A. 1961. John Barber White: Lumberman. Columbia, MO: University of Missouri. 267 p. Ph.D. dissertation.
- Grabner, J.K.; Larsen, D.R.; Kabrick, J.M. 1997. An analysis of MOFEP ground flora: pre-treatment conditions. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 169-197.
- Guyette, R.P. 1993. Report on tree ages at the Eck Tract. Jefferson City, MO: Missouri Department of Conservation.
- Guyette, R.P. 1995. Fire history in the Current River watershed. Missouri Department of Conservation Report. Jefferson City, MO. 74 p.
- Guyette, R.P.; Cutter, B.E. 1997. Fire history, population, and calcium cycling in the Current River Watershed. In: Pallardy, S.G.; Cecich, R.A.; Garrett, H.G.; Johnson, P.S., eds. Proceedings, 11th Central hardwood forest conference; 1997 March 23-26; Columbia, MO. Gen. Tech. Rep. NC-188. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 354-372.
- Guyette, R.P.; Dey, D. 1997. Historic shortleaf pine (*Pinus echinata* Mill.) abundance and fire frequency in a mixed oak-pine forest (MOFEP site 8). In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 136-149.
- Guyette, R.P.; Dey, D.C. 2000. Humans, topography, and wildland fire: The ingredients for long-term patterns in ecosystems. In: Yaussey, D.A., comp. Proceedings workshop on Fire, people, and the central hardwood landscape; 2000 March 12-14; Richmond, KY. Gen. Tech. Rep. NE-274. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 129 p.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandanavian Journal of Statistics. 6: 65-70.
- Hunter, M.L., Jr. 1990. Wildlife, forests, and forestry. Englewood Cliffs, NJ: Prentice Hall. 370 p.
- Kabrick, J.M.; Larsen, D.R.; Shifley, S.R. 1997. Analysis of pre-treatment woody vegetation and environmental data for the Missouri Ozark Forest Ecosystem Project. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 150-168.
- Kile, G.A.; McDonald, G.I.; Byler, J.W. 1991. Ecology and disease in natural forests. In: Shaw, C., III; Kile, G., eds. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture, Forest Service.
- Kozlowski, T.T.; Kramer, J.P.; Pallardy, S.G. 1991. The physiological ecology of woody plants. New York, NY: Academic Press, Inc. 657 p.
- Kramer, J.P.; Kozlowski, T.T. 1979. Physiology of woody plants. New York, NY: Academic Press, Inc. 811 p.
- Krstansky, J.; Nigh, T. 1998. Topographic roughness. Columbia, MO: Missouri Department of Conservation. [unpublished data]
- Krusekopf, H.H.; DeYoung, W.; Watkins, W.I.; Deardorff, C.E. 1921. Soil survey of Reynolds County, Missouri. Washington, DC: U.S. Department of Agriculture, Bureau of Soils. 30 p.



- Kurzejeski, E.; Clawson, R.L.; Renken, R.B.; Sheriff, S.L.; Vangilder, L.D.; Hauser, C.H.; Faaborg, J. 1993. Experimental evaluation of forest management: The Missouri Ozark Forest Ecosystem Project. In: McCabe, R.E.; Glidden, K.A., eds. Transactions of the 58th North American wildlife and natural resources conference; 1993 March 19-24; Washington, DC. Wildlife Management Institute: 599-609.
- Loucks, O. 1970. Evolution of diversity, efficiency and community stability. *American Zoology*. 10: 17-25.
- Meinert, D.; Nigh, T.; Kabrick, J. 1997. Landforms, geology, and soils of the MOFEP study area. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 56-68.
- Nigh, T.; Buck, C.; Grabner, J.; Kabrick, J.; Meinert, D. 2000. An ecological classification system for the Current River Hills Subsection. Jefferson City, MO: Missouri Department of Conservation. 30 p.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science*. 164: 262-270.
- Renken, R.B. 1997. Pre-treatment conditions of herpetofaunal communities on Missouri Ozark Forest Ecosystem Project (MOFEP) sites, 1992-1995. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5, St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 289-308.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*. 43: 223-225.
- SAS. 1989. SAS/STAT user's guide. Version 6, 4th ed. Cary, NC: SAS Institute. 846 p.
- Schurbon, J.M. 2000. Effect of prescribed burning on amphibians in the Francis Marion National Forest, SC. Snowbird, Utah: The Ecological Society of America 85th annual meeting: 200. Abstract.
- Shaw, C.G.; Kile, G.A. 1991. Armillaria root disease. *Agric. Handb.* 691. Washington, DC: U.S. Department of Agriculture, Forest Service. 233 p.
- Sheriff, S.L.; He, Z. 1997. The experimental design of the Missouri Ozark Forest Ecosystem Project. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 26-40.
- Sork, V.L.; Koop, A.; de la Fuente, M.A.; Foster, P.; Raveill, J. 1997. Patterns of genetic variation in woody plant species in the Missouri Ozark Forest Ecosystem Project. In: Brookshire, B.L.; Shifley, S.R., eds. Proceedings of the Missouri Ozark Forest Ecosystem Project symposium: An experimental approach to landscape research; 1997 June 3-5; St. Louis, MO. Gen. Tech. Rep. NC-193. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 231-247.
- Thompson, F.R., III; Dessecker, D.R. 1997. Management of early-successional communities in central hardwood forests. Gen. Tech. Rep. NC-195. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station. 33 p.